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W. D. GUTHRIE

F. F. DICKE

C. R. NEISWANDER

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Ohio Agricultural Experiment Station
Wooster, Ohio

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LEAF AND SHEATH FEEDING RESISTANCE TO THE EUROPEAN CORN BORER IN EIGHT INBRED LINES OF DENT CORN

W. D. GUTHRIE[1], F. F. DICKE[2], and C. R. NEISWANDER[3]

INTRODUCTION

The development of hybrids resistant to the European corn borer, *Pyrausta nubilalis* (Hbn.), has been in progress for over 30 years and has become an integral part of the corn breeding programs in several states and some seed companies. These investigations began when practically all corn grown was open-pollinated. For several years the work on varietal resistance consisted of testing open-pollinated varieties, inbred lines, and hybrids to locate resistant germ plasm.

At the present time the practice of direct extraction of lines from special crosses, commonly referred to as second cycle breeding, and from special synthetic varieties is being used extensively. Agronomically desirable lines with a good level of resistance, even though one of the parents used was susceptible, have been produced with this breeding method. In some instances the procedure of breeding commonly referred to as transference through backcrossing in combination with various methods of intensification or recurrent selection has been used successfully.

Most of the varietal resistance factors studied thus far are most effective against the newly-hatched larvae of the first-brood infestation on corn in the "whorl" stage of growth. Such resistance is usually referred to as resistance to larval establishment and survival. For the European corn borer it is actually resistance to leaf blade feeding. However, some growth inhibiting effects and abnormal mortality have been observed in the third and fourth instar larvae which feed mainly on

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[1]U. S. Department of Agriculture, Agricultural Research Service, Entomology Research Division in cooperation with the Ohio Agricultural Experiment Station, Wooster, Ohio.

[2]U. S. Department of Agriculture, Agricultural Research Service, Entomology Research Division, Ankeny, Iowa in cooperation with Iowa Agricultural Experiment Station, Ames, Iowa.

[3]Ohio Agricultural Experiment Station, Wooster, Ohio.

the midrib and the leaf sheath. The study reported herein was designed to extend our information on both leaf blade and sheath feeding resistance of the first-brood infestation.

REVIEW OF LITERATURE

Three of the earliest reports of differences in borer survival in strains of corn were those of European investigators. Roubaud (1928) artificially infested five French varieties of corn with newly-hatched larvae and found almost complete mortality of larvae on Dent de Cheval. The variety Hâtif d' Auxonne was partially resistant. Roubaud suggested that since the varieties of corn grown in the United States and Canada were more favorable for the development of the corn borer than were the European and particularly the French varieties, the American strains should be replaced by the more resistant European strains. Hase (1929) also found the variety Pferdezahn (Dent de Cheval) to be practically immune to corn borer attack; of 4,368 larvae deposited on 728 plants, less than 1 percent were recovered at harvest. The two German varieties, Baden and Pommern, favored the development of borers.

Ellinger and Chorine (1930, 1931) reported that a South African corn (Natal), which was believed to be of the same origin as Dent de Cheval, was resistant to the corn borer.

In the early research, the differences in borer survival between open-pollinated varieties, inbred lines, or hybrids were thought to be due to the time of planting, to the seasonal habit or size of growth, and the stage of maturity of the corn plant; the early maturing strains of corn were less resistant to attack by the borer than late strains (Felt 1921, Caffrey 1924, Cutright and Huber 1928, Huber *et al.* 1928, Salter *et al.* 1928, Neiswander and Huber 1929, Patch 1929, Kelsheimer and Polivka 1931, Ficht 1936, Meyers *et al.* 1937, Huber 1939).

Meyers *et al.* (1937) reported that Jablonowski, who studied the corn borer for more than 30 years in Hungary, noted, as early as 1898, that early varieties suffered more from corn borer attack than the later varieties; in 1918 early varieties suffered 50 percent greater loss than later varieties. These authors also reported that a Russian, Krassilstchik, noted differences in infestation between varieties in 1914-1915.

One of the early reports on breeding for corn borer resistance was made by Marston (1930a, 1930b, 1931, 1933). The variety Maize Amargo, which is a flint variety developed in Argentina from material believed to have been introduced from Hungary, was observed to be resistant to corn borer attack. This variety was crossed with several native dent varieties. The F_1 generation of these crosses was heavily infested (1930a), leading Marston to believe that susceptibility was dominant and resistance recessive. In the F_2 generation there was a lighter infestation on the plots of Maize Amargo crosses than in the native parent plots. Of 935 F_3 families tested, 227 were not infested. Marston interpreted this as a simple Mendelian ratio of 3 to 1 and believed that the resistance of Maize Amargo was a simple recessive character. Marston (1933) also showed that the resistance of Maize Amargo was transmissible to the progeny of its crosses.

Marston and Mahoney (1933) crossed Maize Amargo with a few varieties of sweet corn in an attempt to select resistant sweet corn types. Lines of Golden Bantam × Maize Amargo were selected which were highly resistant and equal to inbred lines of Golden Bantam in other respects.

In a later article, Marston (1936) reported that Michigan hybrid 561, which had Maize Amargo in its pedigree, was resistant to attack. Patch *et al.* (1938), however, reported this hybrid to be no more resistant in respect to the number of mature borers surviving from a given number of eggs than the susceptible single cross, A × Tr. In all resistance tests reported by Marston and co-workers, the infestation originated from natural oviposition.

Since the early work on resistance, many investigators have discovered that most strains of corn vary somewhat in their comparative resistance and tolerance. The following investigators have reported on differences in relative resistance among open-pollinated varieties, inbred lines, and hybrids: Huber and Herr 1931; Huber 1937; Patch 1937; Patch and Bottger 1937; Thompson 1938, 1939; Huber and Stringfield 1940; Thompson 1940; Patch *et al.* 1941; Pepper and Garrison 1941; Thompson 1941; Huber and Stringfield 1942; Patch *et al.* 1942; Patch and Deay 1948; Patch and Everly 1948; Patch *et al.* 1951. Some of these tests were made under infestations originating from the natural oviposition, whereas others were made under an artificial infestation simulating as nearly as possible natural infestation conditions.

Dicke and Penny (1956) list the source of resistance in new experimental field corn inbreds.

The genetic basis of corn borer resistance has been postulated by several investigators. Patch *et al.* (1942) concluded from tests on a large number of open-pollinated varieties, inbred lines, and dent corn hybrids during the period 1930 to 1939 that the different inbred lines varied in their inherent resistance to survival of the corn borer, and that this resistance was transmitted to hybrids. The authors suggested that resistance was the result of an undetermined number of multiple factors, and that lines showing the greatest degree of resistance contained the largest number of these factors. In these tests the plots were artificially infested, and the number of borers surviving in the summer was determined by dissections. The relative resistance was measured as the percentage deviation of the observed population of borers from the predicted population on the date of silking of the strain of corn.

From a study of 977 sweet corn inbreds, which were artificially infested, Schlosberg and Baker (1948) found that 44 manifested some resistance, and the results obtained from single crosses indicated incomplete dominance of either resistance or susceptibility. The intercrosses of resistant and susceptible parents generally showed results intermediate between those obtained from crosses within resistant and susceptible groups of inbreds.

The results obtained by Singh (1953), in a study of the segregation for leaf feeding differences in the F_2 and first backcross generation of a cross between a resistant and susceptible inbred line, showed a slight tendency for phenotypic dominance of susceptibility. The results also gave an excellent fit to a two-factor pair hypothesis.

Ibrahim (1954) used a large number of chromosomal interchange lines to determine which chromosomes carried genes differentiating the borer resistance of inbred line A411, which was derived from A344 × L317, from the susceptibility of inbred line A344. His data indicated that the resistance of A411 was due to at least one gene in the long arm of chromosome 3, one in the long arm of chromosome 4, and probably one in the long arm of chromosome 5. The resistance of A411 was considered dominant in all crosses studied.

Penny and Dicke (1956) reported on resistance to leaf feeding of a group of F_3 and backcross progenies of a susceptible × resistant cross, M14 × MS1. Segregation of genes for borer resistance at three or more loci with at least partial phenotypic dominance of susceptibility was indicated. In a B14 × N32 cross, one or two gene pairs for leaf feeding resistance were indicated on the basis of individual plant segregations in F_2 and first backcrosses. The F_3 and selfed backcross progeny ratings could not be explained on a single locus basis.

In a later article, Penny and Dicke (1957) reported that ratings of leaf feeding on plants in F_2 and backcross progenies from two susceptible × resistant crosses (the susceptible parents were M14 and WF9; the resistant parent, gl_7 v_{17}, used in both crosses was a stock homozygous for two very closely linked genes, glossy, gl_7, and virescent, v_{17}) indicated that resistance differences were conditioned by segregation of genes at a single locus. The resistance gene was linked with gl_7 v_{17} genes of the resistant parent with cross-over frequencies estimated at from 31 to 37 percent.

The role of chemical substances recovered from the corn plants in inhibiting the growth of larvae has been studied by Beck (1951, 1957a, 1957b), Smissman *et al.* (1957a, 1957b), and Loomis *et al.* (1957). These authors have isolated several chemical factors that inhibit the development of larvae, designated as resistance factors RFA, RFB, and RFC.

Resistance Factor A, 6-methoxybenzoxazolinone, is ether-soluble (Beck *et al.* 1957; Smissman *et al.* 1957a, 1957b; Loomis *et al.* 1957). Neither Resistance Factor B, which is water-soluble, nor Resistance Factor C, which is ether-soluble, have been isolated and characterized (Beck *et al.* 1957).

The inbred lines WF9, W204, W210D, W22, and W22RB were utilized by Beck (1957c) in a study of the role of growth-inhibiting chemical factors in the resistance to the establishment of corn borer larvae. Total resistance factor activity, as determined by bioassay, was reported to be in close agreement with field test ratings of the inbreds. Resistance Factor A was primarily responsible for resistance to leaf feeding on early plant growth stages but negligible after the development of a visible tassel. Resistance Factors B and C contributed about equally to the resistance factor activity found in internode, leaf sheath, husk, and silk tissues.

Painter (1941, 1951, 1954, 1958) and Snelling (1941a, 1941b) discuss the complex of insect resistance in crop plants. These authors list many references on insect resistance.

MATERIALS AND METHODS

Eight inbred lines of dent corn were assembled for a study of their resistance to survival of the first and second larval instars, as expressed by feeding damage to the leaf blade in the whorl stage of development, and their degree of resistance to the third and fourth larval instars, as expressed by feeding lesions on the sheath, midrib, and around the collar. The eight lines were selected on the basis of observed differences in establishment and survival of the first and second larval instars and also on survival of the third and fourth larval instars. However, no quantitative study of resistance of these lines to third and fourth instar larvae has been made. Information on the origin of the lines studied is as follows:

The experimental inbred (W24 × Ind. B2)-2-38-1-Sel. was developed by L. H. Penny and F. F. Dicke at Ankeny, Iowa. W24 is a first cycle line from the open-pollinated variety Golden Daybreak formerly grown in Minnesota. Ind. B2 was developed from Reid yellow dent at the Purdue University Agricultural Experiment Station by R. R. St. John. This line was used in the parent single cross as a source of both moderate leaf feeding and sheath feeding resistance.

W22R was recovered from (W22 × Hy). The recurrent parent (W22) was developed from a single cross (Ill.B10 × W25). Hy, used as the non-recurrent parent, was derived from the variety Illinois High Yield by A. M. Brunson at the Kansas Agricultural Experiment Station and further selected by C. R. Holbert in Illinois after the fifth generation of inbreeding. W22R was developed in Wisconsin by N. P. Neal.

A295 is a direct extraction from (A344 × L317), selection 1088. The original selection was made in an F_3 population by F. F. Dicke in a cooperative resistance breeding project between the U. S. Department of Agriculture and the Minnesota Agricultural Experiment Station from which it was released. Minn. A344 is a sub-strain of Ia. 153 which was derived from the variety Minn. 13. L317 is a derivative from the open-pollinated variety Lancaster Surecrop. Both of these inbreds were originated by M. T. Jenkins at the Iowa Agricultural Experiment Station.

Oh43 is a derivative of (Oh40B × W8), Oh40B being a direct isolate of a composite of eight Lancaster Surecrop lines. W8 is a second cycle inbred derived from (Minn. 13 × Ill. A48) and developed at the Wisconsin Agricultural Experiment Station by N. P. Neal.

Oh51A is a recovered line from (Oh51 × Oh17). Oh51 was used as the recurrent parent and is a derivative of the open-pollinated variety, Clarage. Oh17 was used as the non-recurrent parent and was developed from an ear to row breeding stock. Oh43 and Oh51A were developed by G. H. Stringfield at the Ohio Agricultural Experiment Station.

B14 was developed from a Stiff Stalk synthetic variety by G. F. Sprague at the Iowa Agricultural Experiment Station. This inbred was included because of its outstanding stalk qualities.

M14 was developed by B. E. Moews of Granville, Illinois. It was derived from a single cross (BR10 × R8) and released from the Illinois Agricultural Experiment Station. The origin of BR10 and R8 is obscure.

WF9 was derived from the open-pollinated variety, Reid yellow dent, by R. R. St. John at the Purdue University Agricultural Experiment Station. This inbred is probably the most extensively used inbred in making up commercial hybrids.

These studies were initiated in 1955 and concluded in 1956. With minor exceptions, the experimental methods were similar for the two-year period. The inbred lines were planted in randomized blocks consisting of 26-foot single-row plots with sixfold replication. In order to escape an infestation from the natural moth population, the plots were planted two to three weeks later than normal, depending on seasonal weather conditions.

The experimental plots followed clover in the rotation, and 300 pounds per acre of a 5-10-10 analysis fertilizer were applied in the row before planting. A 33 1/3 percent ammonium nitrate fertilizer was applied as a side-dress application at the rate of 100 pounds per acre when the plants were 12 to 15 inches in extended leaf height.

In 1955 each plant in the experimental plots was artificially infested with six egg masses (approximately 120 eggs), whereas in 1956 the plants were infested with five egg masses (approximately 100 eggs) per plant. The egg masses were incubated to near the hatching stage before being placed in the whorl of the plants.

In 1956 the application of egg masses was made when the plants were in the mid-whorl stage of growth. The height of the inbred lines, as measured from ground level to the tip of the longest leaf, ranged from 27.0 to 32.1 inches. In 1955 the application of egg masses was made when the plants were in a slightly later stage of development. The inbred lines ranged from 27.4 to 36.9 inches in extended leaf height. These tests simulated, as nearly as possible, the natural first-brood infestation.

The pattern of larval survival on the inbred lines was determined by dissecting samples at intervals of 5, 10, 20, and 30 days after egg hatch. In 1955 a four-plant sample was dissected in each plot 5, 10, 20, and 30 days after egg hatch. In 1956 a four-plant sample in each plot was dissected five days after egg hatch, whereas a six-plant sample was dissected 10, 20, and 30 days after egg hatch. The samples on each of the 5-, 10-, 20-, and 30-day intervals were taken at random from all plots in a split-plot arrangement.

Leaf feeding ratings and lesion and burrow counts were made 20 and 30 days after egg hatch.

A nine-class rating scale was used for evaluating borer leaf feeding in the whorl stage of plant development. Only injury caused by larvae feeding in the whorl was used in the leaf rating determinations, i.e., lesions on the sheath collar, sheath, and midrib were not considered in these determinations. In the relative resistance scale, lines which rated 1 to 3 are considered resistant, lines which rated 4 to 6 are considered intermediate in resistance, and lines which rated 7 to 9 are considered highly susceptible. Classification into a resistant, intermediate, or susceptible class is dependent upon the size and shape of leaf injuries, and rating within each class is determined by the number of holes or amount of feeding. A general description of the visual leaf feeding rating classes for evaluating the amount of plant injury for different levels of larval establishment and survival is given in the following summary:

Class 1. No visible leaf injury or a small amount of pin or fine shot-hole type of injury on a few leaves.

Class 2. Small amount of shot-hole type lesions on a few leaves.

Class 3. Shot-hole injury common on several leaves.

Class 4. Several leaves with shot-hole and elongated lesions.

Class 5. Several leaves with elongated lesions.

Class 6. Several leaves with elongated lesions (about 1 inch).

Class 7. Long lesions common on about one-half of the leaves.

Class 8. Long lesions common on about two-thirds of the leaves.

Class 9. Most of the leaves with long lesions.

Examples of classes 1, 5, and 9 are illustrated in Figures 1-3. Dicke (1954) has discussed the biology of the first brood of the corn borer in the corn plant and its relation to the leaf feeding rating system which is important in resistance investigations.

Lesions on the sheath, midrib, and around the collar are caused primarily by the feeding of the third and fourth larval instars. The lesion counts were made on the basis of the number and size of the lesion, i.e., a midrib or sheath lesion 1 to 1½ inches long was counted as one lesion, but a midrib or sheath lesion 6 inches in length was counted as four lesions. Likewise, a lesion which girdled one-third of the collar was counted as one lesion, a lesion which girdled two-thirds of the collar was counted as two lesions, and a lesion which completely girdled the collar, as in Figure 4, was counted as three lesions. This method gave a better index of injury to the midrib, sheath, and sheath collar than is

Fig. 1.—A class 1 visual leaf rating showing small and few lesions caused by young larvae feeding in the whorl. Typical of a resistant reaction to the first-brood corn borers.

possible by disregarding the size of the lesion. Figures 5 and 6 show typical feeding of third and fourth instar larvae on the sheath and midrib.

Fig. 2.—A class 5 visual leaf rating showing several leaves with elongated lesions. Typical of an intermediate reaction to the first-brood corn borer.

Fig. 3.—A class 9 visual leaf rating showing numerous elongated lesions caused primarily by first and second instar larvae feeding in the whorl. Typical of a highly susceptible reaction to the first-brood corn borer.

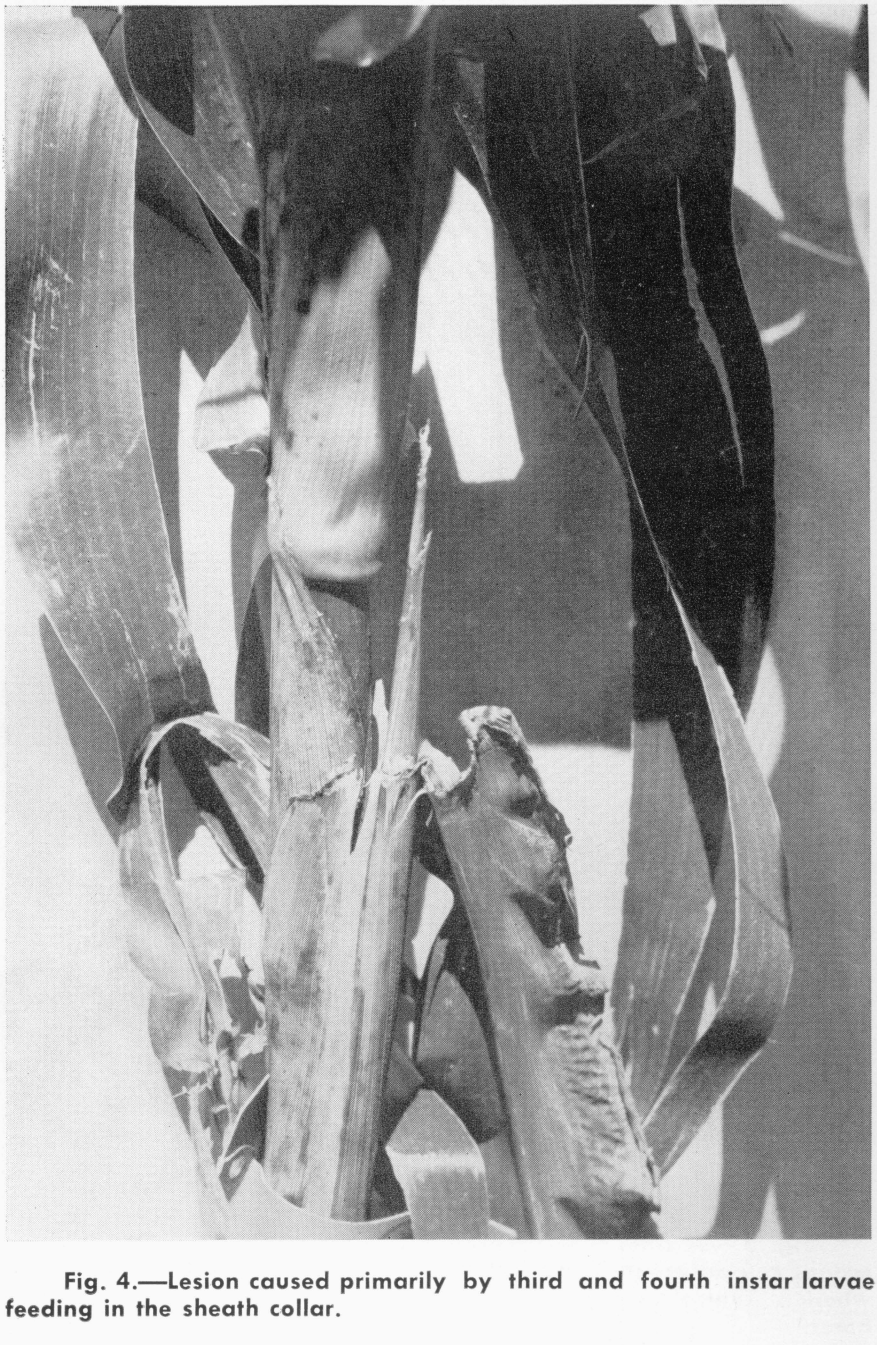

Fig. 4.—Lesion caused primarily by third and fourth instar larvae feeding in the sheath collar.

The methods used in first-brood resistance studies have evolved slowly. During the early work, the criterion used as an index for open-pollinated, hybrid, or inbred line performance was the number of larvae that survived which was usually determined by dissection in late July or

Fig. 5.—Lesions caused primarily by third and fourth instar larvae feeding in the sheath.

early August. This method involved a great deal of work for evaluating only a few hundred entries. Huber (1937) used leaf feeding puncture counts as an index of resistance to first instar larvae. Patch and Everly (1945) used mature larvae in the fall and also leaf feeding ratings (class 0 = least, to 10 = highest infestation level) for evaluating

Fig. 6.—Lesions caused primarily by third and fourth instar larvae feeding in the midrib of the leaf.

a group of inbred lines and hybrids. The leaf feeding rating method and the sheath and midrib lesion count method and combinations thereof were perfected and used on a large scale for evaluating inbred lines and hybrids by F. F. Dicke[4]. A nine-class scale was used for evaluating inbred lines and a five-class scale for evaluating hybrid material (class 1 = least, to 5 or 9 = highest infestation level). He considered the whorl type feeding and also the midrib, sheath, and sheath collar type feeding in the class scale. In tests on hybrids and late generation inbreds, samples of ten plants were usually artificially infested with three or four egg masses (60 or 80 eggs) per plant. The inbreds were rated on a plot basis before pollination. This system preserves the resistant cultures for pollination and progeny testing which is particularly valuable in individual plant selections in segregating populations to study inheritance of resistant factors. This is an excellent method for screening a large amount of material. The highly susceptible material can easily be discovered and discarded. To establish an accurate evaluation of resistance, several tests are essential because activities of several predators may destroy the egg masses or young larvae on certain entries. By using this visual method for evaluation of inbred lines or hybrids, one investigator can test many fold the amount of material as would be possible by dissection. However, for detailed information on the nature of resistance a combination of methods is most desirable.

Since the plots were planted in randomized blocks and the plant dissections were made in a split-plot arrangement, the data on surviving larvae, leaf feeding ratings, and lesion and burrow counts were analyzed according to split-plot procedure (Cochran and Cox 1950). The inbred lines were on the whole plot area, and the dissection intervals of 5, 10, 20, and 30 days after egg hatch were on the split-plot area.

In order to determine the degree of association between surviving larvae, leaf feeding ratings, lesion counts, and burrows, mean values for the lines were used to obtain simple correlation coefficients. Regression coefficients were also computed. By using the means of the six replications in the correlation and regression coefficient determinations, the errors involved in estimating the means were ignored. Larval establishment and survival, resulting from the artificial infestations, were on a much higher level in 1956 than in 1955. Therefore, correlation and regression coefficients were determined for only the 1956 data.

All data were analyzed on a probability per plant basis. The analysis of variance for the data is presented in Appendix Tables 6-8.

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[4]Unpublished data.

EXPERIMENTAL RESULTS

LARVAL ESTABLISHMENT AND SURVIVAL

The data on larval survival, leaf feeding ratings, and lesion and burrow counts obtained in these studies are summarized in Tables 1-5. The conclusions arrived at are based on the two-years' results. However, since a much higher level of larval establishment was obtained in 1956 than in 1955, the data for 1956 give a better picture of what is expected when high populations prevail. In a study of this kind it is imperative to have a high level of larval establishment and survival in order to obtain expression of the resistance factors that exist. The level of larval survival in 1955 was too low to show differences, at the desired magnitude, between inbred lines.

The level of larval survival in the inbred lines in 1956 was satisfactory for evaluating varying levels of resistance by the four criteria: (1) surviving larvae, (2) leaf feeding ratings, (3) lesion counts, and (4) burrows.

TESTS OF DENT CORN INBRED LINES, 1955 AND 1956

The levels of significant differences for the eight inbred lines in 1955 and 1956 are indicated by the usual characters in Table 1. The analysis was based on mean number of larvae, leaf feeding ratings, lesions, and burrows per plant. The analysis of data for 1955 shows significant differences among inbreds, dissection intervals, and the interaction of inbreds × dissection intervals for larvae, significant differences among inbreds for leaf feeding ratings, and significant differences among inbreds and dissection intervals for burrows. There were no significant differences among inbreds, dissection intervals, or the interaction of inbreds × dissection intervals for lesions.

The analysis of data for 1956 shows significant differences among inbreds, dissection intervals, and the interaction of inbreds × dissection intervals for larvae, leaf feeding ratings, lesions, and burrows.

Since the performance of the inbred lines for each dissection interval of 5, 10, 20, and 30 days after egg hatch is of primary interest, the data on the main effect of dissection intervals recorded in Table 2 are of little interest. The over-all effect of inbred lines on larval survival is also of little interest and can be determined by computing means for the dissection intervals of each inbred line, as presented in Tables 3 and 4.

The interaction of inbreds × dissection intervals, which measures the rate of larval mortality, is of greatest interest. These data are reported in Tables 3 and 4 for 1955 and 1956, respectively. Although the analysis of variance for the 1955 data (Table 1) shows significant differences among inbred lines, dissection intervals, and the interaction of inbreds × dissection intervals for larvae, an examination of the data (Table 3) reveals that these differences were due primarily to the differential in larval survival among lines five days after egg hatch. The differences among lines for larvae 10, 20, and 30 days after egg hatch and for leaf feeding ratings, lesions, and burrows 20 and 30 days after egg hatch were small and of minor importance.

Although the level of larval establishment and survival in 1955 was very low, a trend in inbred performance is obvious. B14 (12.3 larvae per plant) followed by WF9 (6.9 larvae per plant) harbored the greatest population five days after egg hatch. W22R, A295, and Oh43 harbored a population of 1.4, 1.9, and 2.3 larvae per plant, respectively, five days after egg hatch, whereas (W24 × B2)-2-38-1, Oh51A, and M14 harbored similar populations of 3.5, 4.0, and 4.0 larvae per plant, respectively. The larval population in all lines decreased appreciably between five and ten days after egg hatch, but did not decrease appreciably from 10 days to 20 and 30 days after egg hatch. By the end of 10, 20, and 30 days after egg hatch there was not much differentiation in larval survival between any of the lines. Although B14 had the highest population five days after egg hatch, the larval population in this inbred decreased rapidly, and at the end of 30 days after egg hatch the population was at a low level.

The low leaf feeding ratings, lesion counts, and burrows for all lines in 1955 resulted from the high larval mortality that occurred within five days after egg hatch; practically all of the larvae had perished by the end of ten days after egg hatch. The larval population was too low in most of the inbreds five days after egg hatch to cause extensive damage to leaf tissue.

A much higher level of larval establishment and survival resulted from the artificial infestation in 1956. Therefore, the resistance effect on the larvae over the 30-day period was measured with more reliability. All four dissection intervals will, therefore, be used as a basis for determining inbred performance. The leaf feeding ratings 20 days after egg hatch and the lesion and burrow counts 30 days after egg hatch will be used as a basis for determining inbred performance. The reason for using only the 20-day leaf feeding ratings and 30-day lesion counts is discussed in a later section entitled "Best Time for Making Leaf Feeding Ratings and Lesion Counts in Resistance Investigations." The following discussion is based on the data recorded in Table 4. The standard error of the means and the differences between inbreds required for significance at the 5 percent probability level are indicated.

The majority of the larvae were in the first and second instar stage of development during the first ten days after egg hatch. Therefore, larval mortality during this period was used as an index to the degree of resistance of the inbred lines to the whorl type of feeding by the first and second instar larvae. Larval mortality between the 10- and 20-day dissection intervals was used as an index to the degree of resistance of the lines to the third and fourth larval instars. However, mortality of the fourth larval instar also occurred beyond 20 days after egg hatch. The majority of the larvae were in the fifth instar stage of development on the 30-day dissection interval.

Based on the four criteria, mean number of larvae, leaf feeding ratings, lesions, and burrows per plant, the experimental inbred (W24 × B2)-2-38-1 was highly resistant to the first and second larval instars. This line may also be resistant to the third and fourth larval instars. However, since the rate of larval mortality was so rapid (only 4.5 larvae per plant survived five days after egg hatch thus resulting in a larval mortality of 95.5 percent), it is difficult to measure the resistance of this line to the feeding of the third and fourth instar larvae. In order to determine conclusively if resistance factors of inbred lines, which are highly resistant to leaf feeding of the early larval instars, are effective against the third and fourth instar larvae, the infestation would have to originate from third instar larvae. There was appreciable larval mortality on this line beyond five days after egg hatch; only 2.7, 1.6, and 1.0 larvae surviving 10, 20, and 30 days after egg hatch, respectively. The fast rate of larval mortality was also reflected in the low leaf feeding rating (1.6 per plant), lesion count (2.4 per plant), and burrows (0.8 per plant) of this line.

W22R was highly resistant to the first and second larval instars. The rate of larval mortality was rapid in this inbred, 4.6 larvae per plant surviving five days after egg hatch; 2.3, 3.0, and 2.4 larvae per plant survived 10, 20, and 30 days after egg hatch, respectively. This line also had a low leaf feeding rating (1.7 per plant) and burrow count (2.5 per plant). However, the lesion count was somewhat higher (4.5 per plant) than would be expected from the fast mortality rate.

A295 was highly resistant to the first and second larval instars. The rate of larval mortality, however, was somewhat slower in A295 than it was in (W24 × B2)-2-38-1 and W22R; 7.7, 3.9, 2.2, and 1.9

larvae per plant surviving 5, 10, 20, and 30 days after egg hatch, respectively. The leaf feeding rating (2.4 per plant) and burrow count (2.8 per plant) were also low for A295. The lesion count (4.2 per plant) was similar to the lesion count for W22R.

Oh43 was resistant to the first and second larval instars but somewhat susceptible to the third and fourth instars. The rate of larval mortality was rather fast but slower than in the three inbreds discussed above; 9.7 larvae per plant surviving five days after egg hatch. As is reflected in the low leaf feeding rating (1.8 per plant), the larval population of 9.7 per plant five days after egg hatch and then a decrease in population to 3.5 larvae per plant ten days after egg hatch was not high enough to cause extensive damage to whorl leaf tissue. However, the larval population of 3.9 and 2.4 per plant 20 and 30 days after egg hatch appears to be high enough to cause considerable damage to the midrib, sheath, and collar as is reflected by the lesion count of 5.6 per plant. Oh43 had 2.8 burrows per plant 30 days after egg hatch.

Oh51A appears to be somewhat susceptible to the first and second larval instars but resistant to the third and fourth instars. The rate of larval mortality was considerably slower than in the four previously discussed inbreds. The larval population of 14.1 and 5.3 per plant five and ten days after egg hatch, respectively, is reflected in an intermediate leaf feeding rating (3.8 per plant). The population died out rapidly beyond ten days after egg hatch, 3.7 and 2.0 larvae per plant remaining 20 and 30 days after egg hatch, respectively, which is reflected in a low lesion count of 2.9 per plant. Oh51A also had a low number of burrows (3.3 per plant).

B14 was highly susceptible to the first and second larval instars. However, it was indicated that this line may be resistant to the third and fourth larval instars. The rate of larval mortality was slow, 21.7 larvae per plant surviving five days after egg hatch. The high number of larvae surviving five days after egg hatch plus the 8.8 larvae per plant, which survived ten days after egg hatch, is reflected in the high leaf feeding rating of 7.0 per plant. On the basis of the high number of larvae which B14 harbored five and ten days after egg hatch, the lesion count of 5.5 per plant is rather low. It appears that this phenomenon is due to the fact that larval mortality in B14 proceeded at a fast rate (5.8 and 3.1 larvae per plant surviving 20 and 30 days after egg hatch, respectively) beyond ten days after egg hatch. Therefore, B14 had almost as low a population 30 days after egg hatch as some of the more resistant lines. B14 also had a relatively low number of burrows (3.0 per plant) which indicates that this inbred is resistant to stalk invasion.

M14 was susceptible to all types of larval feeding. Although the larval population five days after egg hatch (13.9 per plant) was lower in this inbred than in B14 and Oh51A, the population remained at a relatively high level and there was practically no mortality beyond ten days after egg hatch (5.9, 6.3, and 5.2 larvae per plant surviving 10, 20, and 30 days after egg hatch, respectively). The leaf feeding rating, lesion count, and number of burrows were 5.5, 8.3, and 6.9 per plant, respectively.

WF9 was highly susceptible to all types of feeding. This inbred had the highest susceptibility of any line in the test. The rate of mortality was slow (32.5 larvae per plant surviving on the five-day dissection interval). The larval population, consisting of 12.9, 9.8, and 8.9 per plant 10, 20, and 30 days after egg hatch, respectively, remained at a high level and did not decrease appreciably beyond ten days after egg hatch. The high larval population is also reflected in a high leaf feeding rating (7.5 per plant), lesion count (10.4 per plant), and burrow count (8.6 per plant).

Larval mortality in inbred lines, 1955 and 1956.—As is shown in Table 5, most of the larval mortality in the eight inbred lines in 1955 and 1956 occurred during the first few days after egg hatch. This phenomenon has been noted by many investigators and reported by Painter and Ficht (1924), Caesar (1925, 1926), Springer (1930), Huber (1936), and Patch (1943). In 1955 there was appreciable larval mortality in all lines beyond five days after egg hatch but practically no mortality in nearly all of the lines beyond ten days after egg hatch. In 1956 there was appreciable mortality in all lines beyond five days after egg hatch and appreciable mortality in a few lines beyond 10 and 20 days after egg hatch.

Correlation of four criteria for determining corn borer damage.—The data in Table 4 indicate that the eight inbred lines possess different types of resistance and various factors for resistance. The simple correlation coefficients recorded in Figures 7-9 show that on the whole, the four criteria of surviving larvae, leaf feeding ratings, lesion counts, and burrows, for determining corn borer damage or for evaluating inbred lines for corn borer resistance, were equally effective and are highly correlated. Very high correlation coefficients were obtained for larvae 30 days after egg hatch vs. lesion counts 30 days after egg hatch (.95,

Figure 7) and larvae 30 days after egg hatch vs. burrows 30 days after egg hatch (.96, Figure 8). A correlation coefficient of .77 was obtained for larvae 30 days after egg hatch vs. leaf ratings 20 days after egg hatch (Figure 9). Dicke (1954) reported simple correlations of .882 for

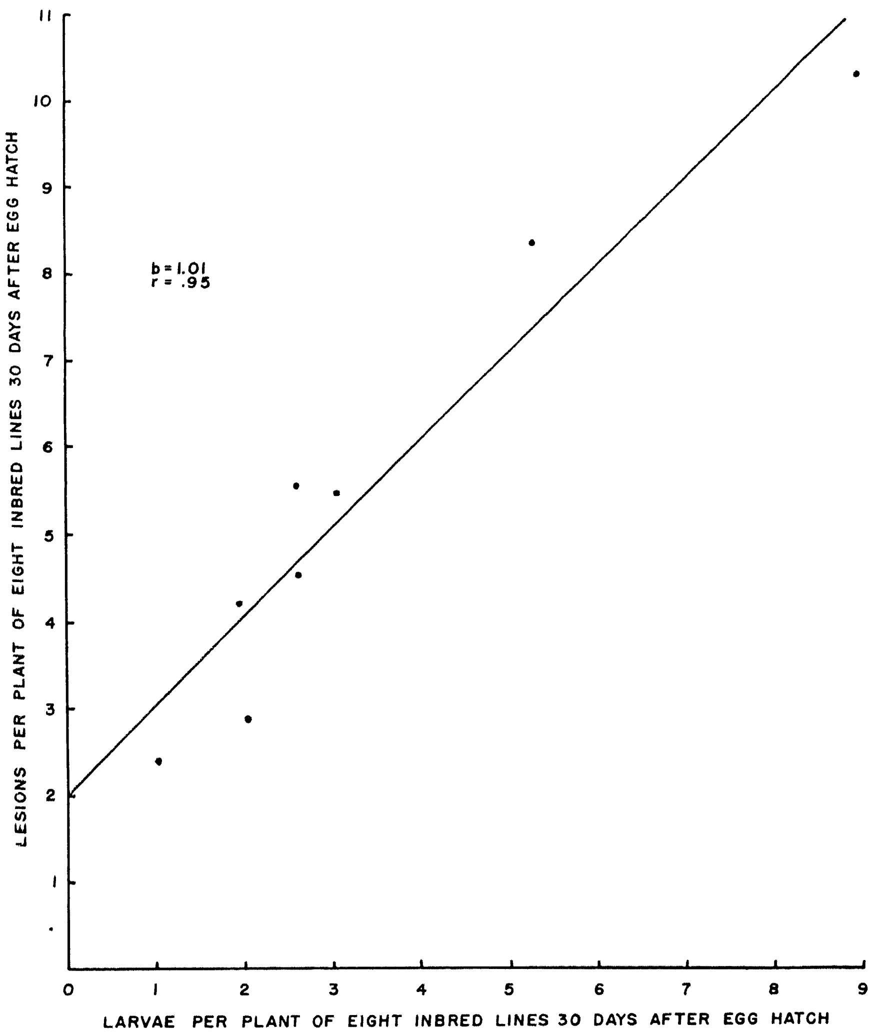

Fig. 7.—Regression and correlation between surviving larvae per plant 30 days after egg hatch and the lesion count per plant 30 days after egg hatch for 8 inbred lines of dent corn, 1956.

larvae per plant vs. leaf rating per plant and .869 for larvae per plant vs. lesions per plant; this study was made with 24 inbred lines. Correlation coefficients which were computed for the 1956 data but not recorded graphically were: lesion counts per plant 30 days after egg hatch vs. burrows per plant 30 days after egg hatch, .93; leaf ratings per plant 20 days after egg hatch vs. burrows per plant 30 days after egg hatch, .75; and leaf ratings per plant 20 days after egg hatch vs. lesion counts per plant 30 days after egg hatch, .72.

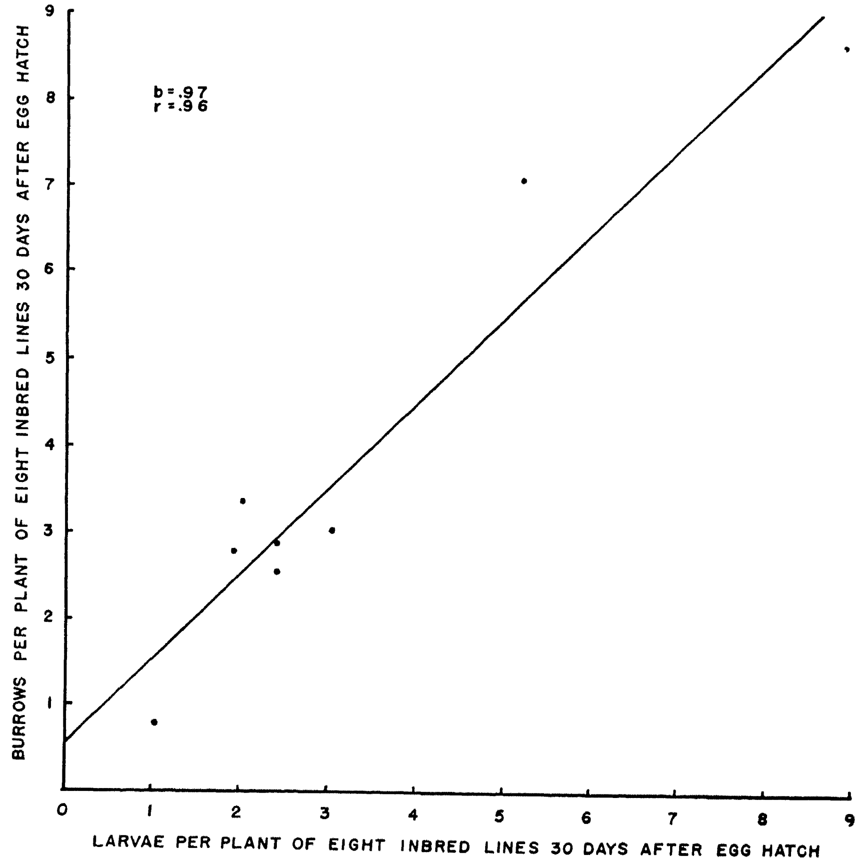

Fig. 8.—Regression and correlation between surviving larvae per plant 30 days after egg hatch and the burrows per plant 30 days after egg hatch for 8 inbred lines of dent corn, 1956.

On the basis of all eight inbred lines, the regression coefficient (b) in Figures 7-9 shows that there was an increase of 1.01 lesions per plant for every increase of 1.00 larva per plant (Figure 7); there was an increase of .97 burrows per plant for every increase of 1.00 larva per plant (Figure 8); and there was an increase of .74 class in leaf feeding rating per plant for every increase of 1.00 larva per plant (Figure 9).

Although the data show high correlations between the four criteria used for determining relative plant damage, certain facets of information in Table 4 should be pointed out. Larvae per plant 30 days or

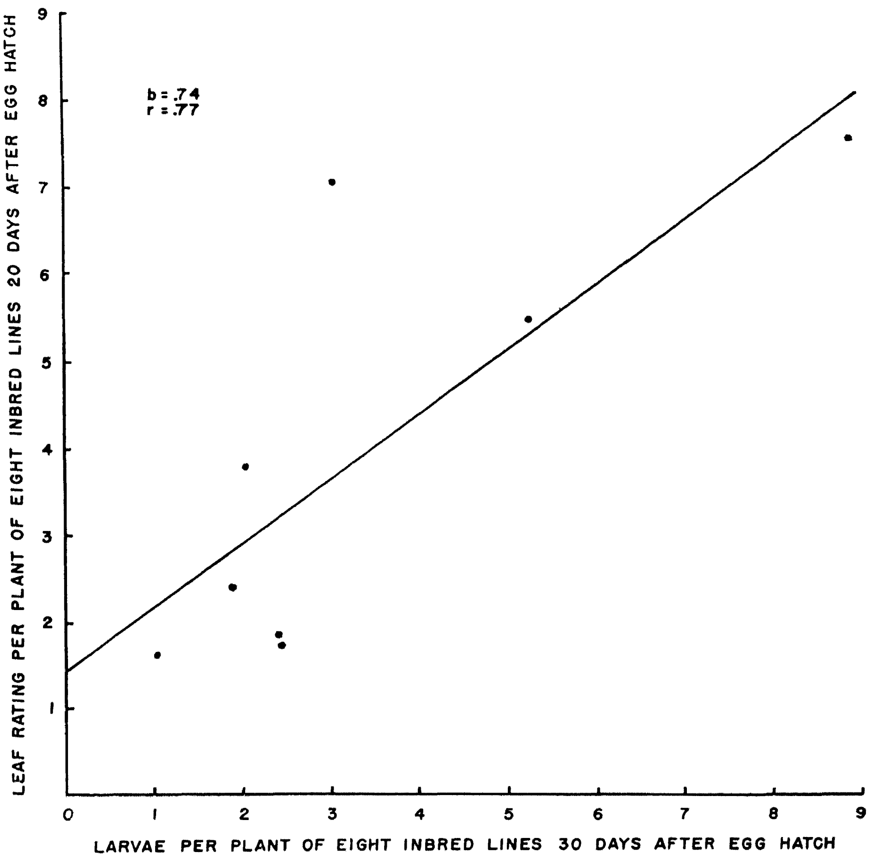

Fig. 9.—Regression and correlation between surviving larvae per plant 30 days after egg hatch and the leaf ratings per plant 20 days after egg hatch for 8 inbred lines of dent corn, 1956.

later after egg hatch may be a good index of inbred performance for some lines but not for others. Likewise, leaf feeding ratings or lesion counts may be a good index of the performance of some lines but not others. Leaf feeding ratings, as an index to the degree of damage caused by first and second instar larvae, and lesion counts, as an index to the degree of damage caused by third and fourth instar larvae, appear to be good criteria for determining the performance of most inbred lines. Larvae per plant 30 days or later after egg hatch would give an inaccurate interpretation of the performance of B14 because the larval population is rather low at this time, and one would conclude that B14 is resistant. However, B14 harbors a high population five and ten days after egg hatch. The larvae feed in the whorl of the plant at this time and if a high population exists, considerable damage is done to leaf tissue. Also the leaf feeding rating used alone as an index to the performance of B14 would be misleading as the rating of 7.0 would indicate high susceptibility. Lesion counts would also be misleading but might be the best single method. With an inbred such as B14, it appears that only a detailed study of the larval survival pattern, leaf feeding rating, lesion count, and burrows would estimate its true performance.

The leaf feeding rating of Oh51A would indicate an intermediate reaction to the early larval feeding, thus a moderately high level of infestation during the first few days after egg hatch, whereas the low lesion count of Oh51A would indicate a fast mortality rate of the third and fourth larval instars. Therefore, the combination of leaf ratings and lesion counts would be a better index to the performance of Oh51A than the larvae surviving 30 days after egg hatch.

A combination of leaf feeding ratings and lesion counts would be as good an index for the performance of W22R, A295, and Oh43 as the larvae surviving 30 days after egg hatch.

These data further indicate that any one of the four criteria of larvae, leaf feeding ratings, lesion counts, and burrows would be equally effective in measuring the performance of inbred lines falling in the extreme classes such as (W24 × B2)-2-38-1, M14, and WF9, i.e., any one of the criteria would indicate that (W24 × B2)-2-38-1 is highly resistant to all types of feeding and that M14 and WF9 are susceptible to all types of feeding.

Vouk (1930) tested certain varieties of corn in Yugoslavia, which were resistant to the European corn borer in certain parts of Europe, and found that the number of larvae surviving from an artificial infestation was practically the same for all varieties, but the damage suffered by the plants, infested with an equal number of larvae, was different for the varieties. From 2.5 to 3.5 larvae per plant were recovered for all varieties in the fall. In two varieties, White-row and Cinquantino, all the plants were broken and dried with poorly developed ears. The stronger and more robust varieties like Pferdezahn were fully matured and showed little injury. The author interpreted this as a constitutional resistance of certain varieties although the susceptibility of the plants to larval infestation was the same. Although the number of larvae recovered by Vouk in the fall was practically the same for all varieties, the rate of mortality must have been much slower in the varieties White-row and Cinquantino. The number of larvae recovered in the fall was a poor index to the comparative performance of the varieties. It appears that leaf feeding ratings and probably lesion counts would have been better criteria for measuring the comparative performance of these varieties.

Best time for making leaf feeding ratings and lesion counts in resistance investigations.—The data in Table 4 show that in these experiments the best time to make leaf feeding ratings of inbred lines is 20 days after egg hatch as the leaves of the plants are closely bunched at this time, and it is easier to visualize the relative amount of leaf damage. In most cases the leaf feeding ratings 30 days after egg hatch were considerably lower than they were 20 days after egg hatch. The best time to make lesion counts is 30 days after egg hatch. The lesion counts were considerably higher on the 30-day dissection interval. However, temperature plays a part in how rapidly the larvae and corn plants develop. In warmer areas these periods might be shortened somewhat.

The results of these investigations show that when evaluating a large number of inbred lines, where the time consumed in dissecting a certain number of plants in each plot is prohibitive, leaf feeding ratings made about three weeks after egg hatch, as an index to the mortality of the first and second larval instars, and lesion counts made from four to five weeks after egg hatch, as an index to the mortality of the third and fourth instar larvae, are good criteria for evaluating the performance of inbred lines. If the time consumed in counting the lesions of a certain number of plants in a plot is prohibitive, a rating scale similar to the one used for leaf ratings could be utilized on a plot basis. F. F. Dicke[5] is investigating the possibility of utilizing a ratio between leaf ratings and lesion counts as an index to inbred performance.

[5]Unpublished data.

TABLE 1.—Summarized analysis of mean number of larvae, leaf feeding ratings, lesions, and burrows per plant of eight inbred lines of dent corn (6 replications). Wooster, Ohio, 1955 and 1956

Source of variation	Larvae		Leaf ratings		Lesions		Burrows	
	1955	1956	1955	1956	1955	1956	1955	1956
Inbreds	**	**	**	**	ns	**	*	**
Dissection interval [1]	**	**	ns	**	ns	**	**	**
Inbred × dissection interval	**	**	ns	*	ns	**	ns	**

* Significant at the 5 percent probability level.

** Significant at the 1 percent probability level.

ns Nonsignificant.

[1] Inbred lines were dissected at intervals of 5, 10, 20, and 30 days after egg hatch.

TABLE 2.—Mean number of larvae, leaf feeding ratings, lesions, and burrows per plant of eight inbred lines of dent corn by dissection intervals (6 replications). Wooster, Ohio, 1955 and 1956

Dissection interval[1]	Larvae		Leaf ratings		Lesions		Burrows	
	1955	1956	1955	1956	1955	1956	1955	1956
5	4.5	13.6	--	--	--	--	--	--
10	1.1	5.7	--	--	--	--	--	--
20	0.9	4.5	1.4	3.9	0.6	2.9	0.4	0.9
30	0.9	3.4	1.2	3.0	0.8	5.5	1.2	3.9
LSD .05	0.77	1.16	ns	**	ns	**	**	**

[1] Days after egg hatch on which the plants were dissected.

TABLE 3.—Mean number of larvae, leaf feeding ratings, lesions, and burrows per plant by inbred line and dissection interval (6 replications). Wooster, Ohio, 1955[1]

Inbred line	Dissection interval[2]									
	Larvae				Leaf ratings[3]		Lesions[4]		Burrows	
	5	10	20	30	20	30	20	30	20	30
(W24 x B2)-2-38-1	3.5	0.2	0.3	0.4	1.0	1.0	0.3	0.5	0.1	0.4
W22R	1.4	0.7	0.7	1.0	1.1	1.0	0.7	0.6	0.4	1.6
A295	1.9	0.2	0.5	0.8	1.0	1.0	0.5	0.7	0.2	1.2
Oh43	2.3	0.9	0.8	0.4	1.0	1.0	0.4	0.8	0.4	0.7
Oh51A	4.0	1.5	1.5	0.9	1.2	1.3	0.9	1.0	1.0	1.4
B14	12.3	1.3	0.9	0.7	2.0	1.3	0.3	0.7	0.1	1.2
M14	4.0	2.4	1.2	1.4	1.1	1.5	0.9	1.2	0.6	1.6
WF9	6.9	1.9	1.4	1.3	2.5	1.7	0.5	0.9	0.4	1.8
Standard error of difference between										
Any two means between dissection intervals for the same inbred	1.09				0.32		0.37		0.41	
Any two means between inbreds for the same dissection interval	1.06				0.37		0.40		0.41	
LSD .05										
Any two means between dissection intervals for the same inbred	2.18				ns		ns		ns	
Any two means between inbreds for the same dissection interval	2.11				ns		ns		ns	

[1] Planted in single row 26-foot plots on May 20.

[2] Number of days plants were dissected after egg hatch (infested with 120 eggs per plant).

[3] The leaf ratings were made on a 9 class basis (class 1 = least, class 9 = highest infestation level).

[4] Lesions refer to feeding damage on the midrib, sheath, and around the collar

TABLE 4.—Mean number of larvae, leaf feeding ratings, lesions, and burrows per plant by inbred line and dissection interval (6 replications). Wooster, Ohio, 1956[1]

Inbred line	Dissection interval[2]									
	Larvae				Leaf ratings[3]		Lesions[4]		Burrows	
	5	10	20	30	20	30	20	30	20	30
(W24 x B2)-2-38-1	4.5	2.7	1.6	1.0	1.6	1.3	1.9	2.4	0.2	0.8
W22R	4.6	2.3	3.0	2.4	1.7	1.1	2.9	4.5	0.4	2.5
A295	7.7	3.9	2.2	1.9	2.4	1.4	1.9	4.2	0.6	2.8
Oh43	9.7	3.5	3.9	2.4	1.8	1.1	3.6	5.6	0.9	2.8
Oh51A	14.1	5.3	3.7	2.0	3.8	1.4	2.3	2.9	0.9	3.3
B14	21.7	8.8	5.8	3.1	7.0	5.7	2.8	5.5	0.6	3.0
M14	13.9	5.9	6.3	5.2	5.5	4.5	4.3	8.3	1.8	6.9
WF9	32.5	12.9	9.8	8.9	7.5	7.6	3.6	10.4	1.5	8.6
Standard error of difference between										
Any two means between dissection intervals for the same inbred	1.66				0.43		0.89		0.45	
Any two means between inbreds for the same dissection interval	1.74				0.33		1.10		0.58	
LSD .05										
Any two means between dissection intervals for the same inbred	3.29				0.86		1.80		0.92	
Any two means between inbreds for the same dissection interval	3.47				0.68		2.23		1.19	

[1]Planted in single row 26-foot plots on June 7.

[2]Number of days plants were dissected after egg hatch (infested with 100 eggs per plant).

[3]The leaf ratings were made on a 9 class basis (class 1 = least, class 9 = highest infestation level).

[4]Lesions refer to feeding damage on the midrib, sheath, and around the collar.

TABLE 5.—Summarized data showing larval mortality as expressed by percent survival on eight inbred lines of dent corn at intervals of 5, 10, 20, and 30 days after egg hatch (6 replications). Wooster, Ohio, 1955 and 1956

Inbred line	Days after egg hatch[1]							
	5		10		20		30	
	1955	1956	1955	1956	1955	1956	1955	1956
(W24 × B2)-2-38-1	3.0	4.5	0.2	2.7	0.3	1.6	0.3	1.0
W22R	1.2	4.6	0.6	2.3	0.6	3.0	0.9	2.4
A295	1.5	7.7	0.2	3.9	0.4	2.2	0.6	1.9
Oh43	2.2	9.7	0.6	3.5	0.6	3.9	0.4	2.4
Oh51A	3.5	14.1	1.2	5.3	1.3	3.7	0.7	2.0
B14	7.8	21.7	1.1	8.8	0.8	5.8	0.5	3.1
M14	3.4	13.9	1.8	5.9	1.0	6.3	1.1	5.2
WF9	5.7	32.5	1.6	12.9	1.2	9.8	1.0	8.9

[1] Each plant in 1955 was artificially infested with 120 eggs, whereas the plants in 1956 were infested with 100 eggs per plant.

SUMMARY

The European corn borer larval survival pattern of eight inbred lines of dent corn, (W24 × B2)-2-38-1, W22R, A295, Oh43, Oh51A, B14, M14, and WF9, was determined at intervals of 5, 10, 20, and 30 days after egg hatch under a uniform simulated natural first-brood infestation (an artificial infestation of 100 to 120 eggs per plant was made in the mid-whorl stage of plant development). Relative leaf feeding ratings, midrib, sheath and collar lesion counts, and stalk burrows were made 20 and 30 days after egg hatch. These investigations were initiated in 1955 and concluded in 1956.

The objective of this study was to extend our information on both leaf blade and sheath feeding resistance of the first-brood infestation.

The level of larval establishment and survival in 1955 was too low to show differences, at the desired magnitude, between inbred lines. The level of larval establishment in the inbred lines in 1956 was satisfactory for evaluating varying levels of resistance by the four criteria of surviving larvae, leaf feeding ratings, lesion counts, and number of burrows.

Based on the four criteria, the experimental inbred (W24 × B2)-2-38-1 was highly resistant to the first and second larval instars. This line may also be resistant to third and fourth instar larvae. The inbreds W22R and A295 were highly resistant to the first and second instars. Oh43 was resistant to the first and second instars but somewhat susceptible to the third and fourth instars, whereas Oh51A was somewhat susceptible to the first and second instars but resistant to the third and fourth instars. B14 was highly susceptible to the first and second instars, but appeared to be resistant to the third and fourth instars. B14 also possessed resistance to stalk invasion. WF9 and M14 were highly susceptible to all types of feeding.

The greatest differential in larval survival between lines was on the five-day dissection interval. Most of the mortality in the eight inbred lines occurred during the first few days after egg hatch.

The results of these investigations indicate that when evaluating a large number of inbred lines, where the time consumed in dissecting a certain number of plants in each plot is prohibitive, leaf feeding ratings (on a plot basis) made about three weeks after egg hatch, as an index to the mortality of the first and second larval instars, and lesion counts made about five weeks after egg hatch, as an index to the mortality of the third and fourth instar larvae, are good criteria for evaluating the performance of inbred lines. If the time consumed in counting the lesions of a certain number of plants in a plot is prohibitive, a rating scale similar to the one used for leaf feeding ratings could be utilized on a plot basis.

Although the four indices for determining corn borer damage were highly correlated, the data show that the number of larvae surviving 30 days or later after egg hatch may be a good index of inbred performance for some lines but not others. The relative leaf feeding rating used alone would also give an inaccurate interpretation of the performance of some lines. A combination of leaf feeding ratings and lesion counts is a good index to the performance of most inbred lines.

APPENDIX

TABLE 6.—Analysis of variance of the data for larvae reported in Tables 2 and 3, 1955 and in Tables 2 and 4, 1956

		1955		1956	
Source of variation	d.f.	Mean square	F	Mean square	F
Whole plot					
Replications	5	5.9488	2.23 ns	61.32	5.25**
Inbreds	7	26.9931	10.11**	481.57	41.20**
Error (A)	35	2.6697		11.69	
Split plot					
Dissection interval	3	152.5246	42.06**	1026.55	123.98**
Inbred × D. I.	21	18.2022	5.02**	74.71	9.02**
Error (B)	120	3.6259		8.28	
Total	191				

**Significant at the 1 percent probability level.
ns Nonsignificant.

TABLE 7.—Analysis of variance of the data for leaf ratings, lesions, and burrows reported in Tables 2 and 3, 1955

		Leaf ratings		Lesions		Burrows	
Source of variation	d. f.	Mean square	F	Mean square	F	Mean square	F
Whole plot							
Replications	5	0.5542	1.08ns	1.0356	1 97ns	1.2631	2.65*
Inbreds	7	1.7827	3.48**	0.5316	1.01ns	1.2950	2.72*
Error (A)	35	0.5120		0.5262		0.4759	
Split plot							
Dissection interval	1	0.4174	1.39ns	1.0817	2.57ns	15.9740	31.41**
Inbred x D. I.	7	0.4905	1.63ns	0.0668	0.16ns	0.5415	1.06 ns
Error (B)	40	0.3005		0.4209		0.5086	
Total	95						

* Significant at the 5 percent probability level.
** Significant at the 1 percent probability level.
ns Nonsignificant.

TABLE 8.—Analysis of variance of the data for leaf ratings, lesions, and burrows reported in Tables 2 and 4, 1956

Source of variation	d. f.	Leaf ratings		Lesions		Burrows	
		Mean square	F	Mean square	F	Mean square	F
Whole plot							
Replications	5	1.1417	1.44ns	19.0178	3.91**	4.0174	2.79*
Inbreds	7	73.3159	92.45**	35.4223	7.28**	28.2924	19.68**
Error (A)	35	0.7930		4.8645		1.4374	
Split plot							
Dissection interval	1	19.8471	36.33**	54.2294	64.55**	215 5203	349.93**
Inbred x D. I.	7	1.6776	3.07*	12.8787	5.39**	13.1810	21.40**
Error (B)	40	0.5463		2.3892		0.6159	
Total	95						

* Significant at the 5 percent probability level.
** Significant at the 1 percent probability level.
ns Nonsignificant.

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